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Various strategies of forelimb movement during contact placing reactions elicited by tactile stimulation of the different aspects of a cat's paw

Julita Czarkowska-Bauch

Department of Neurophysiology, Nencki Institute of Experimental
Biology, 3 Pasteur St., 02-093 Warsaw, Poland,
Email: julita@nencki.gov.pl

Abstract. Forelimb trajectory and the activity of eight muscles operating at the elbow, wrist and digit joints were analyzed during contact placing (CP) reactions elicited by tactile stimuli applied to the lateral (L) or medial (M) side of the cat's forepaw to verify whether a common movement strategy was used in these reactions. A tactile stimulus applied to the lateral side of the paw led, most frequently, to a short-latency activation of the elbow flexor muscles and flexor carpi radialis. Stimulation of the medial side of the paw produced either a short-latency activation of the elbow flexors or both the elbow flexor and extensor muscles. At the distal joints it most frequently activated extensor carpi ulnaris and flexor carpi radialis muscles. Different patterns of activation of the muscles during LCP and MCP reactions led to a diverse involvement of elbow flexion and extension movements at the beginning of the reactions. LCP was usually initiated by the elbow flexion movement whereas during MCP reactions the elbow flexion often appeared with a delay due to a brief co-contraction of the elbow flexor and extensor muscles which temporarily locked the elbow joint. The latter reaction was initiated by a backward/upward movement at the proximal joints accompanied by an ulnar deviation and a palmar flexion of the paw. The medio-lateral components of the movement were also clearly different in LCP and MCP reactions, both at the proximal and distal joints. The results indicate that various strategies of movement are used in CP reactions depending on the site of tactile stimulation.

Key words: contact placing, forelimb muscles, forelimb movements, cat

INTRODUCTION

Contact placing reactions belong to the basic repertory of postural reactions in mammals (Bard 1933). They are elicited by light tactile stimuli applied to the distal part of an unsupported limb which result in a withdrawal of this limb followed by its placement on the touched object (Bard 1933). Contact placing (CP) reactions are widely used to correct a posture when the extremity unexpectedly meets an obstacle, e. g., during stumbling.

In contrast to numerous data concerning the mechanisms of CP reactions elicited by tactile stimuli applied to the dorsum of the paw (dorsal CP), very little information is available about the reactions evoked by tactile stimulation to other sides of the paw. During the dorsal CP reaction a withdrawal of the limb is initiated by shoulder flexion accompanied by a palmar flexion of the paw. Elbow flexion appears with a delay due to a co-contraction of the elbow flexor and extensor muscles at the beginning of the reaction (Czarkowska-Bauch and Bem 1988, Czarkowska-Bauch 1990). This sequence of movements allows effective withdrawal of the limb from the stimulus. A similar strategy of movement has been utilized during a perturbation of the early swing phase of locomotion elicited by tactile stimuli applied to the dorsum of the fore- or the hind paw (Wand et al. 1980, Drew and Rossignol 1985, 1987). In the latter reactions the ankle joint was locked, its flexion was delayed and the reaction started at the proximal and distal joints. All these indicate that a common element of the movement strategy has been involved in the reactions elicited by tactile stimuli applied to the dorsal aspect of the paw (Drew and Rossignol 1985, 1987, Czarkowska-Bauch and Bem 1988, Czarkowska-Bauch 1990). This common reflex might be of spinal origin since it can be elicited by a perturbation of the early swing phase of hind limbs in spinal cats (Forssberg 1979a, Matsukawa et al. 1982). The question arises how tactile stimuli applied to other aspects of the paw will influence the strategy of the movement.

Our aim was to investigate the kinematics and the pattern of activation of the forelimb muscles operating at the elbow and wrist joints during placing reactions elicited by stimulation of lateral or medial aspects of the forepaw and to compare them with those found in dorsal CP reactions (Czarkowska-Bauch and Bem 1988, Czarkowska-Bauch 1990). The data reveal that the location of a tactile stimulus determines the strategy of the movement in CP reactions elicited by stimulation of various aspects of the forepaw.

METHODS

The experiments were carried out on five adult cats of either sex. CP reactions were tested when the animals were placed in a specially designed hammock to which they were well accustomed (Czarkowska-Bauch and Majczyński 1985). All their limbs hung freely. To eliminate placing reactions elicited by visual cues, cats could see neither their limbs nor the experimenter with the stimulator. A daily experimental session lasted about one hour. To elicit the CP reaction the experimenter gently brushed the fur or/and skin over the medial side of the second phalanx (medial CP) or over the ulnar side of the fifth phalanx (lateral CP), in a proximodistal direction, with a tactile stimulator. Also the other skin areas, i. e., around the radial and ulnar sides of the wrist and elbow joints, were stimulated in several experimental sessions to delineate the receptive fields of the medial and lateral CP reactions.

The tactile stimulator consisted of two parallel plates equipped with strain gauges, as described before (Czarkowska and Majczyński 1985). Briefly, a small brush with a high-sensitivity strain gauge was attached to the lower, "stimulating" plate (Czarkowska and Majczyński 1985). Two pulses, one produced at the onset and the other at the termination of a deflection of the brush, corresponded to the onset and termination of the tactile stimulation. A tactile stimulus induced the animal to place the forelimb on the upper, "landing" plate of the stimulator equipped with a strain gauge of a lower sensitivity than the stimulating plate. Contact of the paw with the landing plate also produced an electric pulse. For each analyzed response the duration of the stimulation and the reaction time (i.e., the interval between the onset of the tactile stimulation and the time of contact of the paw with the landing plate of the apparatus) were measured.

The electromyographic (EMG) activity of the following muscles was analyzed: cleidobrachialis (Clb), long and lateral heads of the triceps brachii (LoT and LaT), extensor carpii ulnaris (ECU), flexor carpii ulnaris and radialis (FCU and FCR), and palmaris (Pl). Activity of the biceps brachii (Bi) during medial and lateral CP reactions was described in our previous paper (Czarkowska et al. 1993) but some data were also included in this paper for comparison (see Figs. 3 and 5, Tables I and II).

The EMG activity was recorded with bipolar, stainless steel EMG electrodes which were chronically implanted as described by Loeb and Gans (1986) (see also Czarkowska-Bauch and Bem 1988). The wires were drawn subcutaneously and connected to a multipin contact attached to the skull. The electrodes were implanted under sodium pentobarbital (Nembutal) anesthesia (35 mg/kg i.p.) with Fenactil premedication (1 mg/kg i.m. given 1/2 h. before Nembutal).

The EMG activity was recorded with a differential preamplifier (pass band from 50 Hz to 2,000 Hz) and stored on tape using a 7 channel tape recorder (Racal, Great Britain). For further analysis the stored signals were printed using an EMG recorder (Mingograph, Elema-Siemens) with a time resolution of 10 ms/mm. In the case of fragmented activity, the latencies of the earliest bursts and the times of onset of the later bursts, as well as the duration of all bursts, were calculated. A group of at least three "spikes" was classified as a burst, if it was separated from the next event by 15 ms or more (see Fig. 1B in Czarkowska-Bauch and Bem 1988). The data were normalized, the times of onset and the duration of bursts were then expressed as a percent of the reaction times (i.e., the interval between the onset of the tactile stimulation and the time of contact of the paw with the landing plate of the apparatus).

Movements of the limb during 6 reactions elicited in one cat were filmed, either in parasagittal or in frontal plane, at 64 frames/s with a stationary Bolex 16 mm camera. The position of the spots glued to the fur at the elbow and the wrist and along the limb axis (both on the dorsal and ulnar side of the limb up to 4 cm proximally to the elbow joint) was analyzed for each frame of the film. The horizontal and vertical coordinates of the spots were used to reconstruct the stick figures of the limb and the trajectory of the limb movement. The joint angles were only roughly calculated since the slippage of the skin over the joints might produce a considerable error (Miller and Van der Meche 1975).

RESULTS

Both the medial and lateral CP reactions were elicited regularly (i. e., appeared in over 90% of trials) when the tactile stimulation was applied to the skin over the phalanges. The individual median reaction times of lateral CP reactions were between 310 ms and 475 ms and were usually shorter than those of the medial CP reactions, which ranged from 305 ms to 538 ms. Stimulation of more proximal skin areas was less effective than stimulation of distal skin areas, as in the dorsal CP reactions (Czarkowska-Bauch 1990). Also the reaction times increased when more proximal skin areas were stimulated.

Movements of the forelimb during medial and lateral contact placing reactions

MEDIAL CONTACT PLACING REACTIONS

Medial CP reactions started with a backward displacement of the arm accompanied by a lateral (ulnar) deviation at the wrist (Figs. 1 and 2). These were followed by the arm abduction, an upward movement in the shoulder, a palmar flexion at the wrist and a flexion in the elbow (Fig. 1). Maximal palmar flexion at the wrist was relatively small (about 35 deg.) and it was attained earlier than maximal flexion in the elbow (about 50 deg.). A flexion at the elbow lasted much longer than a palmar flexion of the paw (about 65% and 40% of the reaction time, respectively). The sequence of move-

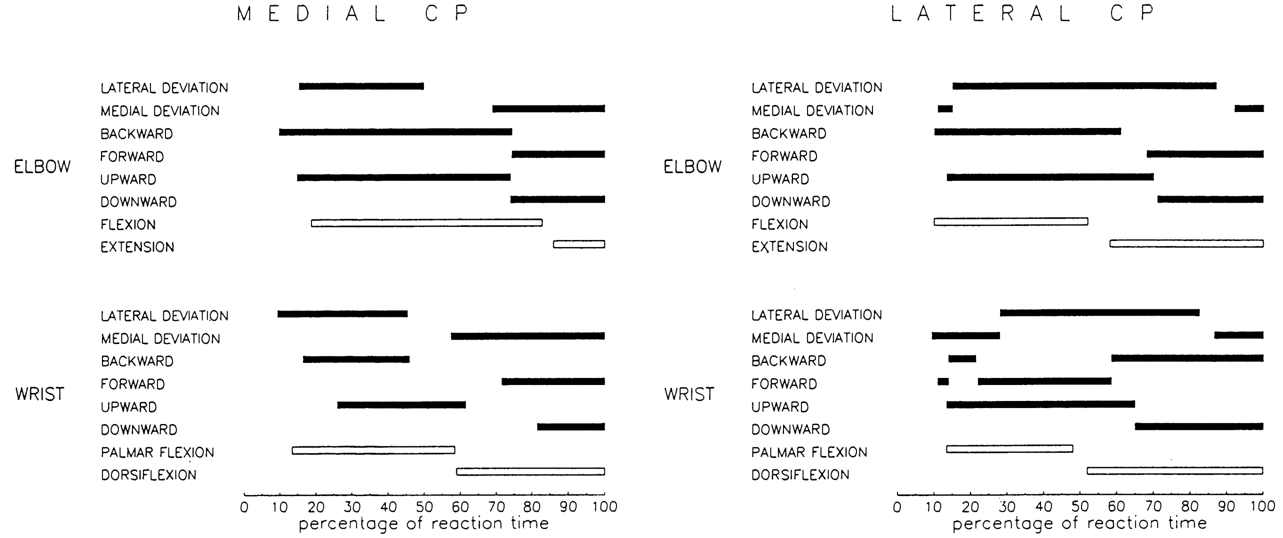

Fig. 1. Onset and duration of kinematic events during two typical medial and two lateral contact placing reactions, expressed as a percentage of the reaction time. Black rectangles represent normalized duration and times of onset of the movements measured from the plots of a horizontal-vertical displacement of the markers placed at the joints. White rectangles represent normalized duration and times of onset of the flexion - extension movements measured from joint angle plots.

ments which led to the placing of the limb on the apparatus was initiated at distal joints by a medial (radial) deviation and a dorsiflexion of the paw. They were followed by arm adduction and downward-forward movement in the shoulder accompanied by an extension in the elbow (Fig. 1). A dorsiflexion at the wrist started earlier than a corresponding extension in the elbow and the wrist became almost straight while the elbow remained flexed.

LATERAL CONTACT PLACING REACTIONS

Lateral CP reactions started with a flexion in the elbow accompanied by a medial deviation of the paw (Figs. 1 and 2). These movements were followed by a brief forward displacement of the wrist and adduction of the arm accompanied by a long-lasting backward displacement of the arm. A long-lasting abduction and an upward displacement of the arm with a palmar flexion of the paw proceeded later (Fig. 1). The latter sequence of movements was accompanied by a brief backward-forward displacement of the wrist and by a long-lasting lateral deviation of the paw (Fig. 1). A flexion in the elbow developed rapidly, as indicated by an early forward displacement of the wrist joint during a lifting of the forelimb (Figs. 1 and 2). Maximal flexion in the elbow

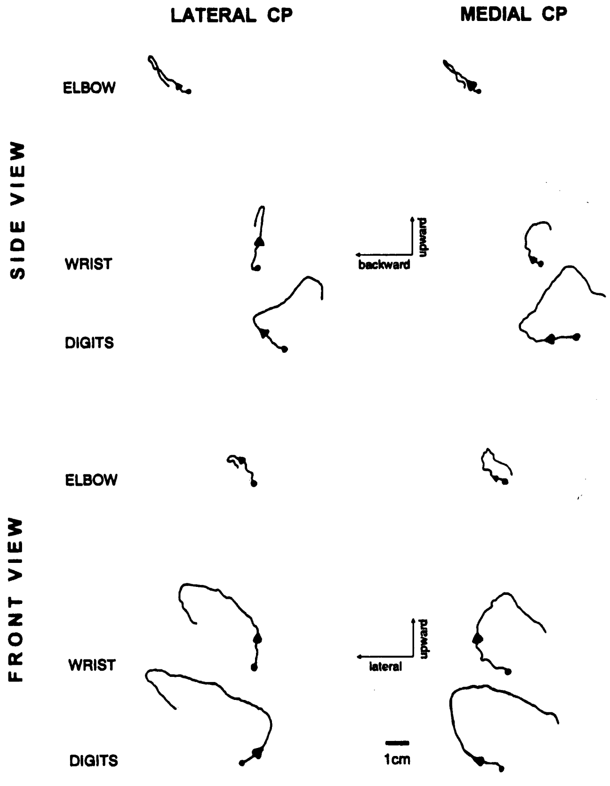

Fig. 2. The trajectory of the digits, wrist and elbow of the right forelimb during two typical, complete lateral and two medial contact placing reactions reconstructed, frame by frame, from the film. The initial position of the joints was treated as a stationary reference point. Solid dots indicate the onset of movement. Solid arrowheads show direction of the limb movement in relation to the longitudinal body axis.

(about 50 deg.) was attained later than corresponding palmar flexion at the wrist (approximately 30 deg.).

The sequence of movements which led to the placing of the limb on the apparatus started with a dorsiflexion at the wrist, a backward displacement of the wrist and an extension in the elbow followed by a forward-downward displacement of the arm.

Medio-lateral components of that movement were complex (Figs. 1 and 2). Early medial deviation of the paw corresponded to the beginning of raising of the limb. It was accompanied by a brief adduction followed by a long-lasting abduction in the shoulder and by a lateral deviation of the paw. The beginning of a downward movement was still associated with arm abduction and with a lateral deviation of the paw. Late adduction of the arm, preceded by a medial deviation of the paw, appeared at the end of a final sequence of movements. As in other CP reactions, changes in the paw contour on the consecutive frames of the motion picture (not illustrated) suggest that these were also accompanied by the rotation of the forearm.

COMPARISON OF THE FORELIMB MOVEMENTS DURING MEDIAL AND LATERAL CP REACTIONS

The most pronounced differences between movements of the forelimb during medial and lateral CP reactions appeared at the beginning of lifting of the limb (Figs. 1 and 2). During medial CP reactions, an upward movement of the forearm progressed gradually with a clear backward displacement, while during lateral CP a raising of the forearm appeared with a forward displacement of the wrist joint indicating that it was due to a flexion in the elbow (Figs. 1 and 2). The other difference arises from various involvement of the medio-lateral components of movements during medial and lateral CP reactions. Figure 2 shows that the trajectory of the wrist during medial CP might be approximated by a circle while that of the elbow by an ellipse, with a counterclockwise rotation (in relation to the animal's body axes). In contrast, during lateral CP, the trajectory of the forelimb might be approximated by an ellipse with a clockwise rotation (Fig. 2).

Muscle activity during medial and lateral contact placing reactions

The EMG activity of all tested muscles was usually fragmented, with a variable number of bursts (Fig. 3). The muscle activity appeared first in the elbow flexor muscles which also showed the most stable patterns of activation. The greatest vari-

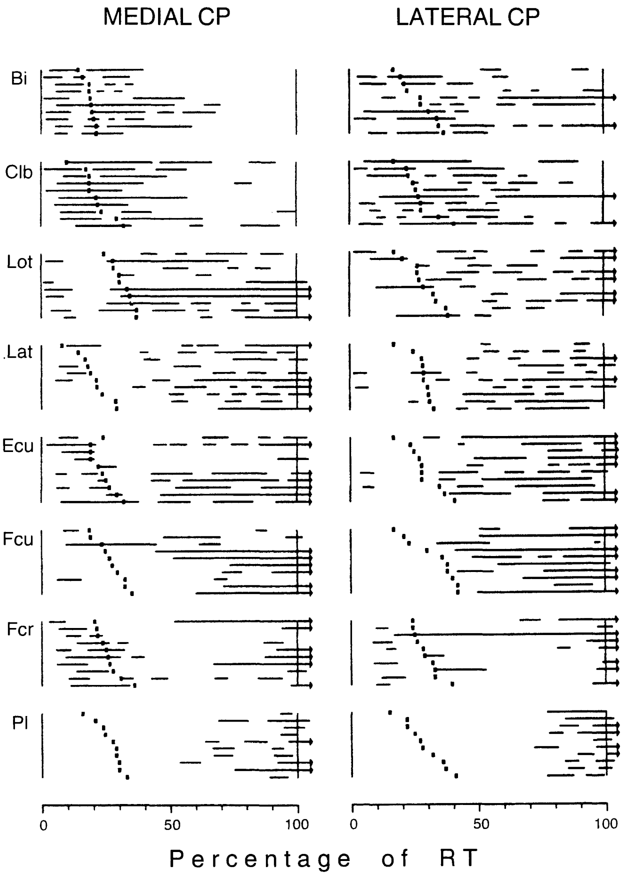

Fig. 3. Patterns of activation of eight forelimb muscles during ten typical medial and ten lateral contact placing reactions. Only CP reactions with the reaction times close to the individual median values were analyzed. Each bar indicates the onset and the duration of EMG activity of the respective muscle during one reaction expressed as a percentage of the reaction time. Dots indicate the termination of tactile stimulation (normalized). Abbreviations: Bi, biceps brachii; LaT and LoT, lateral and long heads of the triceps brachii, respectively; ECU, extensor carpi ulnaris; FCU, flexor carpi ulnaris; FCR, flexor carpi radialis; Pl, palmaris. The arrows indicate that muscle activity lasted more than 50 ms after the limb has been placed on the apparatus.

ability of responses appeared in the elbow extensor muscles.

MEDIAL CONTACT PLACING REACTIONS

The arm and the elbow flexor activity

Clb responded to stimulation of the medial aspect of the paw with the latencies between 19 and 34 ms (individual median values, Table I). Its main activity occupied the first 50% of the reaction time but in a small fraction of the CP reactions Clb was active also in the later phase of the reaction (Fig. 3). Figure 4 shows a unimodal distribution of the latencies of Clb activity. The times of onset of the second burst of Clb activity were more variable than those of the first ones (Table I, Fig. 4). In the majority of reactions, the first burst of Clb activity appeared during the first 15% of the reaction time while the second one started between 15% and 35% of the reaction time (Fig. 4). The total duration of Clb activity varied between 48 and 124 ms which corresponded to between 13% and 38% of the reaction time (individual median values; Table I). The responses of Clb were more variable than the previously reported activity of the biceps brachii (Czarkowska-Bauch et

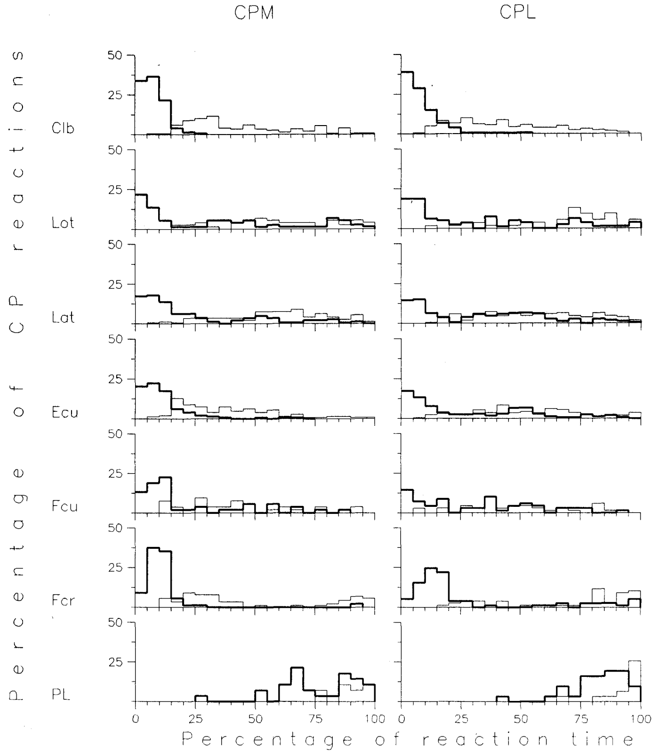

Fig. 4. Examples of the distributions of the onsets of the first (thick line) and the second (thin line) burst of the activity of the various muscles in one animal during medial (CPM) and lateral (CPL) contact placing reactions. The data are expressed in percents of the reaction time. Other explanations as in Fig. 3.

TABLE I

Activity of the forelimb muscles during contact placing reaction elicited by tactile stimulation of the medial aspect of the paw. Number of bursts of EMG activity, their onset and duration - individual median values or their range. The bold numbers indicate that the differences between EMG parameters were significant (*P*<0.01 - Smirnov-Kolmogorov and Median tests), at least in 50% of animals

Muscle	N	n	Bursts (n)	First burst latency	First burst duration	First burst latency	First burst duration	Total duration
				(ms)		(ms)		(ms)
Bi	2	321	3	12-18	29-34	92-100	48-61	126-170
Clb	4	466	2	19-34	24-58	94-136	24-51	4-124
LaT	3	463	2-3	48-207	24-27	179-285	19-31	92-140
LoT	3	257	1-2	46-175	14-68	210-279	19-29	48-119
ECU	5	642	2-4	24-48	1929	97-252	29-39	143-291
FCU	4	403	1-2	39-63	29-68	121-213	27-63	83-160
FCR	1	87	2	34	29	111	24	58
pl	1	28	1	204	19	233	22	24

Abbreviations: N, number of animals; n, number of elicited CP reactions; (n), number of bursts of EMG activity.

al. 1993). Also the latencies of Clb were longer than those of Bi (Table I).

The elbow extensors activity

Both LoT and LaT muscles were mainly active during the last 60% of the reaction time, i.e., before the onset of the extension of the elbow (Fig. 3). However, in over 40% of CP reactions they were also activated at the beginning of the reactions (Figs. 3 and 4). The short latency and short-lasting responses were within the same range as for the elbow flexors and they coincided with the first 10%-15% of the CP reaction time (Figs. 3-5). The times of onset of the second burst were highly variable in both muscles (Fig. 4). The total duration of LaT and LoT activity ranged from 92 to 140 ms in LaT and from 48 to 119 ms in LoT (individual median values) which corresponded to between 17% and 33% and between 10.5% and 30% of the reaction time, respectively (Table I).

Relations between the elbow flexor and extensor activity

Clb and LoT were frequently coactivated during the initial period of the medial CP, i.e., between 5% and 40% of the reaction time (Fig. 5). Their coactivation was associated with a retraction and elevation of the shoulder accompanied by an abduction of the arm. On the other hand, the other pair of the antagonistic muscles acting at the elbow, Bi and LaT, were less frequently coactivated during medial CP (Fig. 5). This is in line with the observation that only in about 50% of medial CP reactions the initial elbow flexion was delayed due to a co-contraction of the antagonistic muscles acting at the elbow joint.

Muscles operating at the wrist

ECU responded to tactile stimulus applied to a medial aspect of the paw with a short-latency and short-lasting period of activity (Fig. 4). This initial response was followed by a long-lasting activity which started with a short delay after the stimulus had terminated. The early phase of ECU activity contributed to the lateral deviation of the paw and it appeared during the early phase of medial but not lateral CP reactions (Fig. 3). The late period of ECU activity was, presumably, associated with a dorsiflexion at the wrist since it started before and lasted throughout this movement (Figs. 1 and 3). The late activity continued over various periods of time after the paw was placed on the apparatus (Fig. 3). ECU was activated with latencies similar to those of the

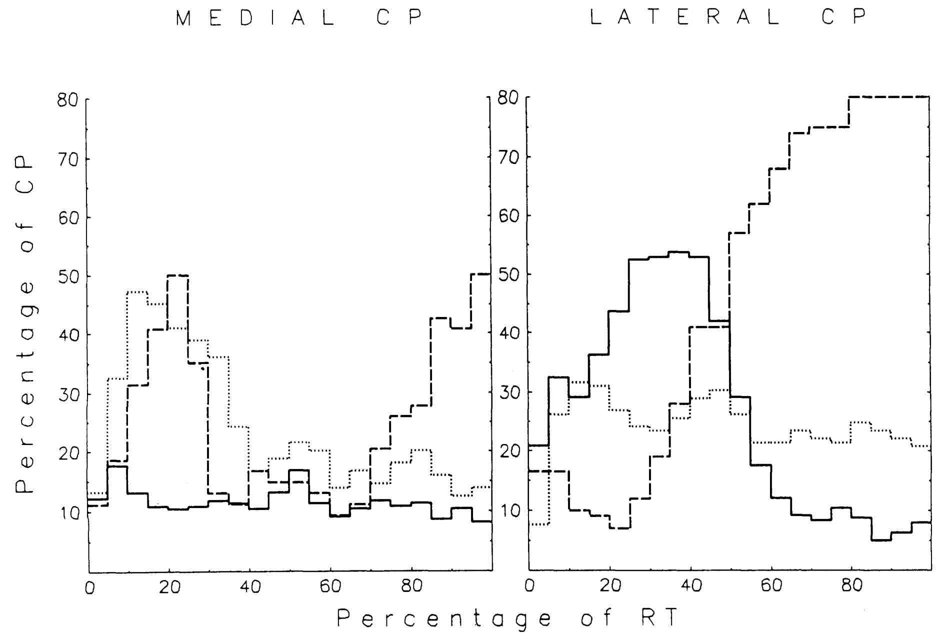

Fig. 5. Normalized distributions of coactivations of EMG activity of two antagonistic muscles operating at the elbow (Bi and LaT, solid line and Clb and Lot, dotted line) and at the wrist (ECU and FCU, dashed line) during over 150 medial and over 150 lateral contact placing reactions. The activity of the two pairs of muscles was recorded simultaneously. The data are expressed in percents of the reaction time.

elbow flexors, which coincided mainly with the first 15% of the reaction time, but the times of onset of the second burst of ECU activity showed some variability (Table I, Fig. 4). ECU was the most frequently active among all the tested muscles during medial CP reactions and the total duration of its activity was the longest (Table I). It usually corresponded to about 50% of the reaction time.

In about 40% of the reactions FCU activity started with the latencies during the first 15% of the reaction time (Figs. 3 and 4). In the remaining reactions the latencies were longer (Table I, Fig. 4). It was in line with a weak involvement of a palmar flexion of the paw in the early sequence of movements of medial CP reactions, as indicated by a small maximal palmar flexion movement during these reactions. The times of onset of the second burst of FCU activity were variable (Table I, Fig. 4). The later period of FCU activity was associated with the landing of the limb on the apparatus (Figs. 1 and 3). FCU was also frequently active during the reaction and the total duration of its activity corresponded to about 41% of the reaction time.

The initial phase of FCR activity appeared between the first 10% and 40% of reaction time and corresponded to a palmar flexion of the paw, while the late phase of activation coincided with the last 20% of the reaction time and was associated with the landing of the paw on the apparatus (Fig. 3). FCR responded to tactile stimulus with latencies of unimodal distribution (Fig. 4). Generally, this muscle was not very active during the reaction and the total duration of its activity was about 60 ms (median values) which corresponded to about 17% of the reaction time (Table I). In most cases FCR activity continued after the paw was placed on the apparatus. (Fig. 3).

Pl muscle was activated mainly at the end of the reaction to contribute to the landing of the limb on the apparatus (Figs. 1 and 3). Its activity started with a long-latency of about 200 ms and continued after the paw was placed on the apparatus (Table I, Fig. 3). The total duration of its activity occupied about 10% of the reaction time.

Relations between the wrist flexor and extensor activity

Figure 5 shows that ECU and FCU were coactivated in two phases of the reaction. They were frequently coactivated at the beginning of the reaction, i. e., between 10% and 30% of the reaction time and at the end of the reaction. The early coactivation might be attributed to a simultaneous lateral deviation and palmar flexion of the paw. ECU and FCU

TABLE II

Activity of the forelimb muscles during contact placing reaction elicited by tactile stimulation of the lateral aspect of the paw. Other explanations as in Table I

Muscle	N	n	Bursts (n)	First burst latency (ms)	First burst duration (ms)	First burst latency (ms)	First burst duration (ms)	Total duration (ms)
Bi	2	349	3	19-28	48-58	127-133	48-61	160-194
Clb	4	488	2-3	19-41	24-51	114-175	24-51	63-147
LaT	3	522	1-3	95-146	24-48	172-285	19-31	63-184
LoT	3	261	1-2	116-184	17-29	213-298	19-29	58-136
ECU	5	640	2-4	29-78	19-48	131-167	29-39	136-254
FCU	4	300	1-2	70-174	39-61	184-254	27-63	65-203
FCR	1	76	2	48	19	267	19	46
pl	1	31	1	238	17	257	19	24

Abbreviations: N, number of animals; n, number of elicited CP reactions; (n), number of bursts of EMG activity.

were also coactivated at the end of the reaction when the paw was about to land on the apparatus.

LATERAL CONTACT PLACING REACTIONS

The arm and the elbow flexor activity

The responses of Clb to stimulation of the lateral aspect of the paw were generally longer than those of Bi (Table II). Both muscles were active longer during lateral than medial CP reactions (Tables I and II). Activity of Clb was widely distributed during the reaction and contributed to various phases of the reaction (Figs. 1 and 3). Figure 4 shows a unimodal distribution of the latencies of Clb activity. The times of onset of the second burst of Clb activity were more variable than those of the first ones (Table II, Fig. 4). The duration of Clb activity corresponded to between 16% and 40% of the reaction time (individual median values).

The elbow extensors activity

LaT and LoT were activated in a similar way during lateral CP and their activity occupied the last 50% of reaction time (Fig. 3). Both muscles responded with longer latencies to tactile stimulation of the lateral than medial side of the paw (Figs. 3 and 4; Tables I and II). The total duration of LaT and LoT activity corresponded to between 16% and 41% of the reaction time in LaT and from 12% to 36% in LoT (individual median values).

Relations between the elbow flexor and extensor activity

Figure 5 shows that during lateral CP reactions Bi and LaT, the antagonists acting at the elbow joint, were rarely coactivated during the initial 20% of the reaction time but they became frequently coactivated between 20% and 55% of the reaction time. Their coactivation corresponded to a transition between a lifting of the limb and the initial sequence of movements leading to a placing of the limb on the apparatus (Figs. 1 and 5). This indicates that a flexion at the elbow joint developed at the very beginning of the reaction, before the elbow flexor and extensor muscles were coactivated. The other pair of antagonists, Clb and LoT, were also coactivated during lateral CP reactions but less frequently than Bi and LaT (Fig. 5). The frequency of their coactivation was multimodal and distributed throughout the reaction time (Fig. 5).

Muscles operating at the wrist

ECU responded with longer latencies to stimulation of the lateral than of the medial aspect of the paw (Tables I and II). Its long-lasting activity started after the stimulus had terminated and occupied the last 60% of the reaction time (Fig. 3). The longer latencies of ECU activity during lateral rather than medial CP reactions corresponded to a later involvement of the lateral deviation of the paw in the former than in the latter reactions (Figs. 1 and 3). Also during lateral CP reactions ECU was the most frequently active among all the tested muscles (Table II). The late activity continued over various periods of time after the paw was placed on the apparatus (Fig. 3).

FCU was active mainly during the last 50% of the reaction time (Fig. 3). Latencies of FCU were much longer during lateral than during medial CP reactions (Figs. 3 and 4, Tables I and II). Activity of that muscle during lateral CP was mainly associated with a landing of the paw on the apparatus (Figs. 1 and 3). The total duration of its activity corresponded to between 20% and 55% of the reaction time.

FCR muscle responded to stimulation of the lateral aspect of the paw in two distinct periods (Fig. 3). The early phase of its activation appeared mainly between the first 10% and 30% of the reaction time and corresponded to a palmar flexion of the paw. The late phase coincided with the last 20% of the reaction time and was associated with the landing of the paw on the apparatus. The total duration of FCR activity corresponded to about 13% of the reaction time.

Pl was activated mainly at the end of the reaction to contribute to the landing of the limb on the apparatus (Figs. 1, 3 and 4). Its activity started with a long latency of about 200 ms and continued after the paw was placed on the apparatus (Table II). The total duration of its activity corresponded to about 10% of the reaction time.

Relations between the wrist flexor and extensor activity

Figure 5 shows that ECU and FCU muscles were coactivated during different phases of the reaction than antagonistic muscles operating at the elbow. ECU and FCU were strongly coactivated at the end of the reaction and became highly synchronous only when the limb was near to landing on the apparatus.

Relations between dorsal, lateral and medial CP reactions

The results show that a tactile stimulus applied to the lateral side of the paw led, most frequently, to a short-latency activation of the elbow flexor muscles and FCR. In contrast, when the stimulus was applied to the dorsal side of the paw it activated both the elbow flexor and extensor muscles. At the distal joints it led to a short-latency activation of ECU, FCU and FCR muscles (Czarkowska-Bauch and Bem 1988, Czarkowska-Bauch 1990). Stimulation of the medial side of the paw produced either a short- latency activation of the elbow flexors or of both the elbow flexor and extensor muscles. At the distal joints it activated most frequently ECU and FCR muscles.

Different patterns of activation of the muscles acting at the elbow and the wrist joints led to various strategies of the forelimb movements. In one of them, characteristic for the movements elicited by tactile stimuli addressed to the dorsal and partly to the medial side of the paw, the movement started at the proximal and distal joints and the elbow flexion was delayed due to an early co-contraction of the elbow flexor and extensor muscles. The difference appeared at the distal joints since during dorsal CP the reaction started with a palmar flexion of the paw while during medial CP it was initiated by ulnar flexion at the wrist. In contrast, when the tactile stimulus was applied to the lateral side of the paw the movement started with the elbow flexion and a medial deviation of the paw.

During medial and dorsal CP reactions the elbow flexion movement started later and lasted longer (about 65% of the reaction time) than during lateral CP (about 44% of the reaction time). The elbow extension movement was less involved in the medial and dorsal CP reactions than in the lateral CP and it lasted about 15% and 43% of the reaction time, respectively.

The medio-lateral components of the movements accompanied all the reactions but they were more pronounced during medial and lateral than during dorsal CP reactions, both at the proximal and distal joints.

Generally, movements of the forelimb during lateral CP were more complex than during medial and dorsal CP reactions. Figure 1 shows that during the initial 30% of the lateral CP, four transitions from the ongoing to the opposite movement appeared at the elbow and wrist joints (e.g., from a flexion to extension). All these transitions were very fast. In contrast, they were observed neither in the medial nor in dorsal CP reactions (see Fig. 1; Fig. 3 in Czarkowska-Bauch 1990).

DISCUSSION

Different patterns of muscle activity at the elbow and the wrist joints as well as different time-tables of the kinematic events during medial, lateral and dorsal CP reactions indicate that various strategies of movement were used in these reactions depending on the site of tactile stimulation. In one of them, characteristic for the dorsal CP reactions, a backward-upward movement at proximal joints accompanied by a palmar flexion and lateral deviation at the wrist joint initiated the reaction. The elbow flexion followed this sequence of movements with some delay. A similar strategy was observed in about 50% of the reactions elicited by stimulation of the medial aspect of the paw. Another strategy of movement was used when the reaction was elicited by stimuli applied to the lateral aspect of the paw. Lateral CP was initiated with a flexion at the elbow joint accompanied by a medial deviation of the paw. A backward-upward movement accompanied by an adduction of the arm appeared later.

The question arises whether different strategies of movement in CP reactions evoked by tactile stimulation of various surfaces of the paw are necessary when the animal overcomes an obstacle. A strategy of movement, which locks the elbow joint at the beginning of the dorsal and partly of the medial CP reactions allows the cat to withdraw the forelimb from the touched object easier than when the elbow flexion movement starts simultaneously with movements at the proximal and distal joints. The early flexion at the elbow would bring the wrist joint closer to an obstacle. Thus, a bigger movement at the proximal and distal joints would be required to compensate it. It is clear that when an obstacle appears at the lateral side of the forelimb, the early elbow flexion does not interfere with the obstacle. Together with a medial deviation of the paw and adduction of the arm it allows the cat to withdraw the limb efficiently from a touched object. Such a strategy was used during lateral CP reactions.

There are hardly any other data available to which the present results on the strategy of movements in cats during CP reactions elicited by tactile stimulation of various aspects of the forelimb can be compared. A vast majority of the data concerning postural reactions elicited by light tactile stimulus are related to the reactions elicited by stimuli applied to the dorsal aspects of the forelimb (Drew and Rossignol 1985, 1987, Batson and Amassian 1986). Generally, the latencies and duration of the first responses of all muscles tested by us during medial, lateral and dorsal CP reactions were longer than those to a tap to the dorsum of the paw during swing phase of locomotion observed by Drew and Rossignol (1987). This might suggest that an interaction between the ongoing locomotor muscle activity and the reflex muscle responses to tactile stimulation leads to a reduction of the effect of perturbation on locomotor activity. Also the type of mechanical stimulation might influence the timing of the muscle responses. During CP reactions tactile stimulation lasted longer than a tap used during perturbation of locomotion (Drew and Rossignol 1987).

The possibility that CP evoked by contact with the lateral side of the forelimb differs from the medial or dorsal CP reactions has been discussed by some authors (Amassian et al. 1972, Amassian and Ross 1978, Amassian 1979, Villablanca and Olmstead 1979, Yu 1983) on the basis of the delayed appearance of lateral rather than dorsal or medial CP during ontogeny or a longer recovery of the lateral than dorsal or medial CP reactions following CNS lesions. Lateral CP was found to be selectively depressed by cooling the sensorimotor cortex, internal capsule or bulbar pyramids in two week old kittens (Amassian and Ross 1978). In adult cats, lateral CP of the forelimb recovered later than the dorsal or medial CP following lesions of VA-VL nuclei of the thalamus (Amassian et al. 1972). After unilateral neodecortication, conditioned CP reactions recovered only to contact with the medial or dorsal but not with the lateral aspects of the paw (Yu 1983). All these data indicate some differences between dorsal, medial and lateral CP reactions.

The presented results indicate that tactile stimuli applied to various aspects of the paw change both the timing and the pattern of activation of the elbow flexor and extensor muscles and also in different ways activate the distal muscles. It is possible that tactile stimuli of a various location activate different subsets of spinal interneurons on their way to appropriate motoneurons. There are several examples of such "private pathways" or "specialized reflexes" elicited by cutaneous afferents of the plantar aspect of the foot or the skin area overlying the extensor muscles in the hind limb (Hagbarth 1952, Engberg 1964, Lundberg 1967, 1972). Recently, it was also found that cutaneous excitation of flexor digitorum longus motoneurons was controlled in a different way when stimuli were addressed either to the dorsal or to the plantar aspect of the paw (Moschovakis et al. 1991). Our results indicate that one can also expect different control of the triceps brachii as well as of the flexor and extensor carpi ulnaris motoneurons by tactile stimuli applied either to the dorsal, medial or lateral aspect of the paw.

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